

Phyllotaxis and Stem Vascularization of *Dampiera* R.Br. (Goodeniaceae)

M. T. M. RAJPUT and R. C. CAROLIN

RAJPUT, M. T. M., and CAROLIN, R. C. Phyllotaxis and stem vascularization of *Dampiera* R.Br. (Goodeniaceae). *Proc. Linn. Soc. N.S.W.* 107 (4), (1983) 1984: 479-485.

Three types of phyllotaxis are described in the genus *Dampiera*: distichous (1/2), tristichous (1/3) and pentastichous (2/5). The stems of those species having the first two types of phyllotaxis also have cortical bundles while those having pentastichous phyllotaxis do not. The lateral leaf traces are derived from the cortical bundles when the latter are present. The sequence of the derivation of the leaf traces is described for the different types of phyllotaxis. The phyllotaxis and stem vascularization have proved to be significant taxonomic characters.

M. T. M. Rajput, Department of Botany, University of Sind, Shah Abdul Latif Campus, Khairpur, Sind, Pakistan, and R. C. Carolin, John Ray Herbarium, School of Biological Sciences, University of Sydney, Australia 2006; manuscript received 19 October 1982, accepted for publication in revised form 20 July 1983.

INTRODUCTION

Differences in the stem anatomy of *Dampiera* have been recognized by previous workers, particularly in regard to the presence of cortical bundles (Krause, 1912) but neither these nor the phyllotaxis have been emphasized as a taxonomic feature of any importance. Nevertheless, both sets of attributes have proved useful in recognizing infra-generic groupings and the differences are reported here.

MATERIAL AND METHODS

Transverse sections of the young vegetative buds of fresh material of representative species of *Dampiera* were cut after fixation in formalin-acetic-alcohol and embedding in paraffin wax. The apex of the stem is so small that it was necessary to use buds in which the leaves showed fairly significant development to determine the phyllotaxis.

For the study of stem vascularization serial sections were cut individually and drawn with a *camera lucida*. The vascular connections were determined by comparing the individual successive drawings.

This investigation was supplemented by clearing young and old stems of dried material. The stems were bleached with a commercial sodium hypochlorite solution, washed and cleared in aqueous chloralhydrate (50g chloralhydrate, 25g lactic acid, 25g phenol). Sometimes the vascular strands were not well displayed at this stage and instead of mounting them in chloralhydrate they were stained in 10% aqueous safranin and dehydrated in absolute alcohol. The stems were transferred to a mixture of 75% polylyte 61-209 resin diluted with 25% acetone. After one to four hours in vacuum the material was passed through two or three changes of pure resin and left to set in moulds with catalyst no 2 (MEKP). Both resin and catalyst were supplied by A. C. Hatrick Pty Ltd, Australia. The blocks could be examined using a stereo-microscope.

Phyllotaxis terms are used as defined by Richards (1948). The terms used to describe the stem anatomy are those proposed by Dormer (1950, 1972). Cortical bundles are those which are present outside the stele as separate bundles in the cortical region of the stem and which supply lateral organs. A trace is a single vascular bundle which, at its upper end, passes out from the stele into some lateral organ without further considerable addition or subtraction of the vascular material.

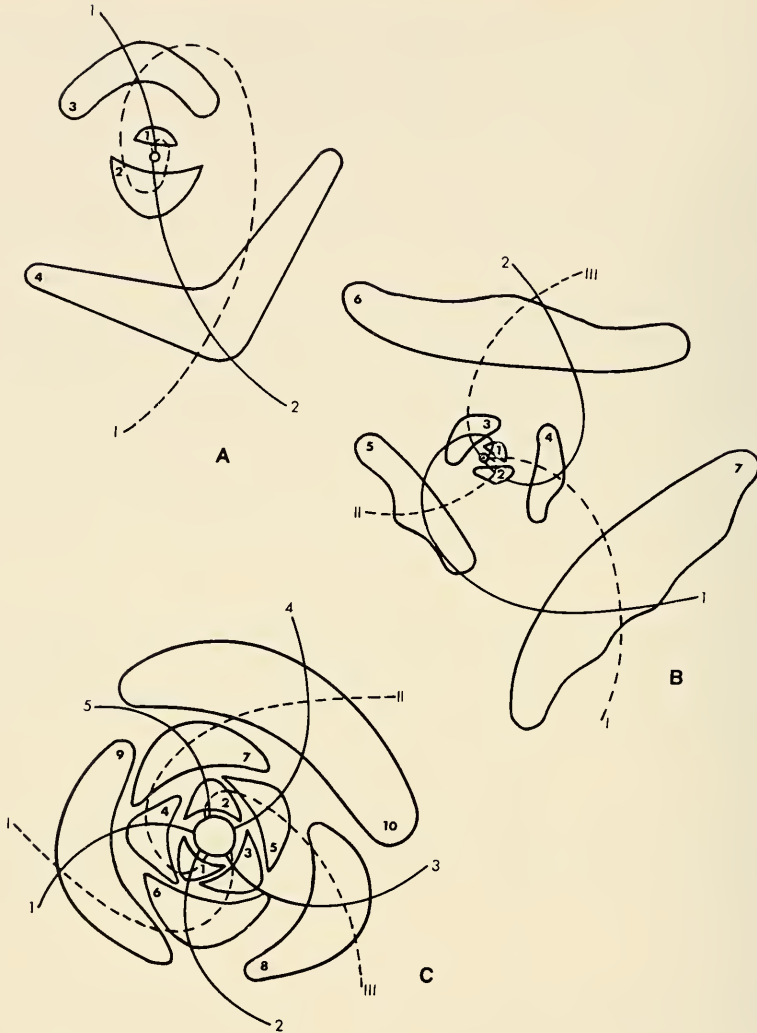


Fig. 1. Sections of leaves and stems near the tips of stems showing phyllotaxis ground plans: A. *D. alata*, sect. *Campptospora*; B. *D. stricta*, sect. *Dicoelia*; C. *D. cinerea*, sect. *Linschotenia*.

RESULTS

LEAF PHYLLOTAXIS

As the leaves are always spirally arranged it is always possible to draw a spiral through the median lines of successive leaves. The angle between the median lines of successive leaves is the angle of divergence and, according to Richards (1948) is constant for any one plant. The phyllotaxis ratio is a fraction of the circumference of the stem. The numerator of the fraction is the number of revolutions of the stem that are necessary to reach the next leaf of the same orthostichy, the denominator the number of plastochrones passed over until this leaf is reached. Three different types of phyllotaxis can be recognized in *Dampiera*.

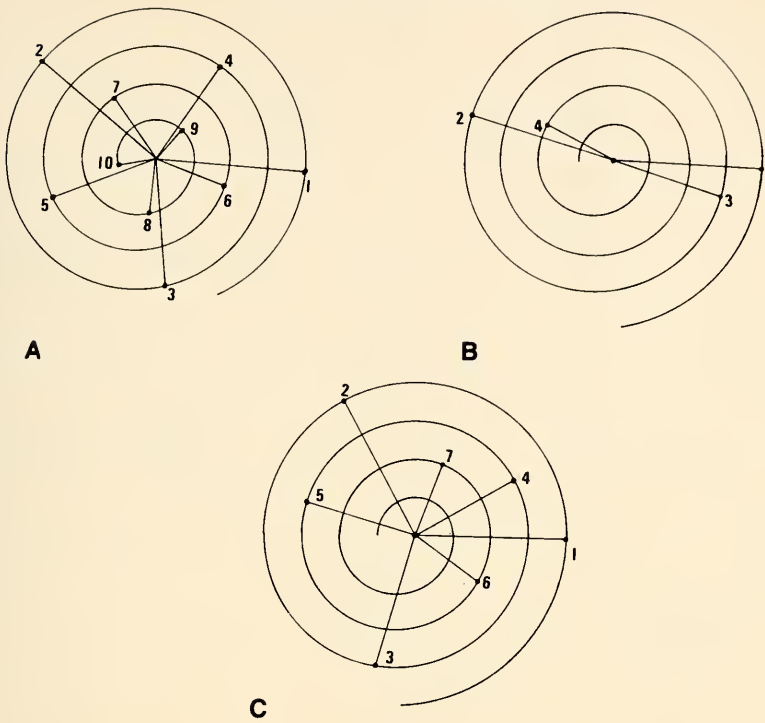


Fig. 2. Diagrammatic representation of phyllotaxis: **A.** *D. alata*; **B.** *D. stricta*; **C.** *D. cinerea*.

1. $1/2$ or distichous phyllotaxis. e.g. *D. alata*. only two orthostichies are recognized. The mean angular divergence is 171° and there are (1 + 2) parastichies (Figs 1A, 2A) (see Church, 1904).

This type of phyllotaxis occurs in those species with a flattened stem and two cortical bundles.

2. $1/3$ or tristichous phyllotaxis, e.g., *D. stricta*.

Three orthostichies can be recognized, the mean angular divergence is $131^\circ 2'$ and there are (2 + 3) contact parastichies (Figs 1B, 2B). This type of phyllotaxis is found in those species with triangular stems and three cortical bundles.

3. $2/5$ or pentastichous phyllotaxis. e.g., *D. cinerea*.

Five orthostichies can be recognized with a mean angular divergence of $135^\circ 2'$ and there are (3 + 5) contact parastichies (Figs 1C, 2C). This type of phyllotaxis is found in the species with ribbed or unribbed stems without cortical bundles.

Fresh material of the section *Cephalantha* was not available and the rosette arrangement of the leaves made it impossible to determine the phyllotaxis of any species of this section.

STEM VASCULARIZATION

In almost all the leaves of *Dampiera* species there are three traces, one median although it may not be strictly median in position, and two lateral. The departure of the cortical bundles and the bundles of the stele to the leaves of representative species of *Dampiera* are shown in Fig. 3. The single line surrounding the bundles of the stele

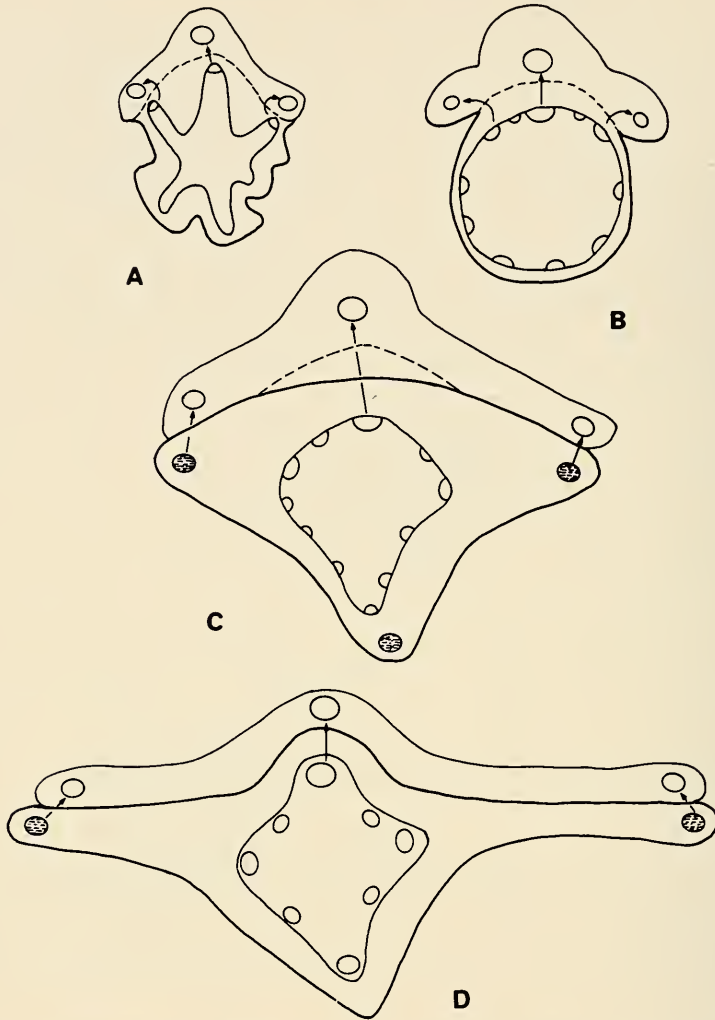


Fig. 3. Schematic transverse section showing origin of vascular traces of leaves from bundles of stems: **A.** *D. alata*; **B.** *D. stricta*; **C.** *D. oligophylla*, sect. *Dampiera*; **D.** *D. cinerea*.

represents a well-defined boundary between sclerenchyma (of the stele) and parenchyma (of the cortex) of small regular cells which are assumed to be the starch sheath.

In order to describe the stem vascularization it was necessary to develop some simple diagrammatic representation of the stem as shown in Fig. 4. The cortical vascular system of the stem is represented as though it has been cut open on one side and then laid out flat. The small circles represent lateral foliar traces and the large circles represent median foliar traces which latter are derived from the stele directly as shown in Fig. 3. Since both lateral and median traces are derived from the stele in *D. oligophylla*, the stelar traces are shown for this species only.

Cortical vascular bundles are absent in all members of sect. *Dampiera*, sec. *Cephalantha*, and sect. *Linschotenia* that have been examined to date, and the foliar traces are supplied directly from the stele at each node.

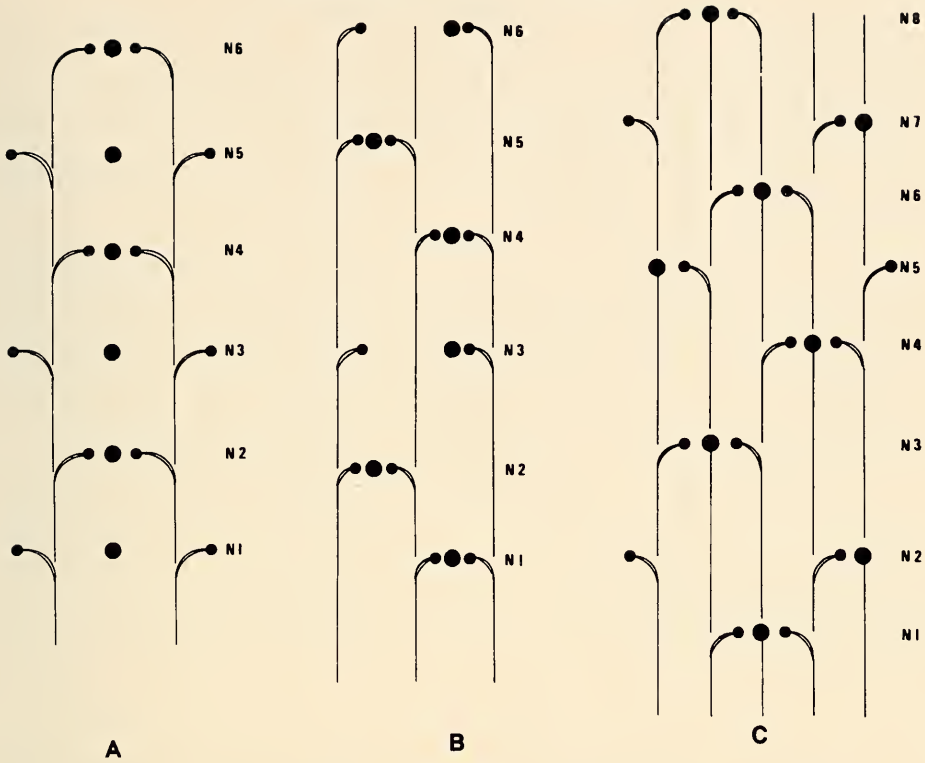


Fig. 4. Diagrams showing the successive origins of vascular strands of leaves from those of the stem: A. *D. alata*; B. *D. stricta*; C. *D. oligophylla*. For explanation see text.

Except for *D. angulata*, the members of sect. *Camptospora* which have been examined here, e.g., *D. lindleyi* have two cortical bundles (Fig. 3A), and each passes into the leaf at each node and forms a lateral trace. A median trace is supplied directly from the stele at each node. At the same time two new cortical bundles develop from the stele and then supply the leaf on the next node with the lateral traces, thus each cortical bundle in the stem passes through only one internode. The position in the stele from which the cortical bundles are supplied is the same on nodes two and four (Fig. 4A). The leaf vascular supply from the stele of the stem at each node is consistent with the phyllotaxis.

In the members of sect. *Dicoelia* the stem has three cortical bundles and the number of the stelar bundles varies from six to nine in the internode. The case of a stem having three cortical and six well-developed vascular bundles has been examined, e.g., *D. stricta* (Figs 3B, 4B). Only two of the three cortical bundles take part in the vascular supply of the leaf at each node. One passes through two internodes and the other through only one internode whilst the median trace is supplied directly from the stele at each node (Fig. 4B). Two of the six vascular bundles which are present in the stele supply the median trace of the leaf at each node and these two stelar bundles always pass through two internodes (Fig. 4B).

The new cortical bundle which passes through two internodes is succeeded by a newly developed cortical bundle which passes through only one internode whilst the

cortical bundle which passes through one internode is succeeded by a bundle which passes through two internodes. The position in the stele from which the cortical bundles are supplied is the same at nodes 1, 4 and 7 (Fig. 4B). The position of the vascular supply at each node of the stem is consistent with the 1/3 phyllotaxis.

In ribbed stems the cortical bundles are absent but the stele is convoluted and the individual bundles correspond to the ribs, e.g., *D. oligophylla* ssp. *oligophylla* (Fig. 3C). In the unribbed stems the cortical bundles are also absent and the vascular bundles of the stele do not usually protrude into the cortex, e.g., *D. cinerea* (Fig. 3D).

In sect. *Dampiera* the number of the vascular bundles of the stele which protrude into the cortex varies from five to nine. The case of a stem having five well-developed vascular bundles has been examined. Three of the five vascular bundles which protrude into the cortex take part in the supply of the leaf at each node, one to the median trace and two to the laterals. The vascular bundle which forms the median trace subsequently always passes through two internodes and then forms a lateral trace, subsequently the same bundle passes through one internode to form another lateral trace and after that through two internodes to form a median trace (Fig. 4C).

The position in the stele from which the vascular bundles are supplied is the same on nodes 1, 6 and 11. This is consistent with the 2/5 phyllotaxis. This type of vascular supply is also found in members of sect. *Linschotenia*. The stems of members of this section, however, are unribbed and have a narrow cortex with an unconvoluted stele (Fig. 3D). Since the members of sect. *Dampiera* have ribbed stems with a wide cortex and stelar bundles protruding into the cortex, this constitutes the main difference in the anatomy of the two sections.

DISCUSSION

A number of elegant ways of describing phyllotaxis have been devised (see Williams, 1975), but virtually the only effective way for taxonomic work remains the well-established phyllotaxis ratio since most apices are so small that it is usually impossible to determine angles of divergence and plastochrone ratios or a generative angle (Thomas and Connell, 1980) at the primordial level. Such is the case with *Dampiera* and leaf initials further away from the apex have to be used for these determinations. There is thus some risk of displacement of these leaves during embedding and cutting.

Several apices each of *D. stricta* and *D. purpurea* were examined. The mean angle of divergence remained constant indicating that displacement in the horizontal plane was insignificant. However, the plastochrone ratio did vary and was considered to be unreliable.

The types of phyllotaxis and stem vascularization clearly have some taxonomic significance. We will deal elsewhere in detail with the taxonomy (Rajput and Carolin, in prep.) and the phylogeny of the genus but some conclusions can be drawn on the information presented here.

Sect. *Dicoelia* in fact consists entirely of species with cortical bundles and 1/3 phyllotaxis. Sect. *Camptospora* consists of species with both triangular and flattened stems also all with cortical bundles and 1/2 or 1/3 phyllotaxis. The implication is that these two sections are more closely related to each other than either is to the other three sections, none of which has cortical bundles. There is thus a clear dichotomy in the genus since even in species such as *D. oligophylla* where the young stems are triangular, they do not possess cortical bundles.

There is also clearly a very close connection between the vascularization and phyllotaxis, which indeed one would expect.

ACKNOWLEDGEMENTS

John Ford helped with the preparation of the sections, Bill Sansom drew the schematic diagrams and Belinda Pellew helped considerably in checking the text and figures. We should also like to thank Dr L. A. S. Johnson for providing some of the fresh material and particularly we should like to thank Saleha Tahir for helpful discussions.

References

- CHURCH, A. H., 1904. — *On the relation of phyllotaxis to mechanical laws*. Oxford: Williams and Norgate.
- DORMER, K. J., 1950. — Observations on the vascular supply to axillary branches. *New Phytol.* 49: 36-39.
- , 1972. — *Shoot organization in vascular plants*. London: Chapman and Hall.
- KRAUSE, K., 1912. — Goodeniaceae und Brunoniaceae. *Das Pflanzenreich*, Bd. 54. Berlin: Engelmann.
- RICHARDS, F. J., 1948. — The geometry of phyllotaxis and its origin. *Symposium of the Society for experimental Biology*. Cambridge: Cambridge University Press.
- THOMAS, R. L., and CONNELL, M. G. R., 1980. — The generative spiral in phyllotaxis theory. *Ann. Bot.* 45:237-249.
- WILLIAMS, R. F., 1975. — *The shoot apex and leaf growth*. Cambridge: Cambridge University Press.